The Role of Migratory Waterfowl as Nutrient Vectors in a Managed Wetland

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Abstract: Dense aggregations of waterfowl, often caused by loss of native wetlands and increased waterfowl numbers, can result in the destruction of wetland vegetation and agricultural crops, increase the risk of infectious disease outbreaks, and decrease water quality. Problems related to water quality may be particularly severe in arid regions of the southwestern United States, where water quality and quantity are contentious issues. Over 40,000 Lesser Snow Geese (Chen caerulescens caerulescens) and Ross' Geese (Chen rossii) winter annually at Bosque del Apache National Wildlife Refuge, New Mexico. Daily feeding bouts by geese move large quantities of nutrients from farm fields where they feed to managed wetlands where they roost. Using energy and mass balance models, population estimates, daily and seasonal migration patterns, and feeding behaviors, we estimated the mass and ratio of nitrogen to phosphorus of nutrients loaded by geese into the wetlands of the Bosque del Apache National Wildlife Refuge. Loading rates peaked in late November 1995 at more than 300 kg nitrogen per day and over 30 kg phosphorus per day. As feeding behaviors changed through the winter and bird densities declined, loading rates fell. Our estimates suggest that in the winter of 1995–1996, bird-borne nutrients supplied nearly 40% of the nitrogen and 75% of the phosphorus entering the primary wetland used for geese roosting. High loading rates by geese are a consequence of their colonial roosting behavior; over 90% of the geese roost on 10% of the wetland area. The effects of nutrient loading could be reduced by increasing flushing rates or dispersal of roosting waterfowl. The loss of natural wetlands, however, limits options for expanding wetland area available to waterfowl, and it may be difficult to increase flushing rates in this arid region. Thus, management of waterfowl and the nutrients they move will continue to be an important issue for wetlands of wildlife refuges.

El Papel de las Aves Acuáticas como Vectores de Nutrientes en un Humedal Manejado

Resumen: Densas agregaciones de aves acuáticas causadas frecuentemente por la pérdida de humedales nativos y el incremento en el número de ace acuáticas, puede resultar en la destrucción de la vegetación de humedales y cultivos, un incremento en el riesgo de dispersión de enfermedades infecciosas y una disminución en la calidad del agua. Los problemas relacionados con la calidad del agua pueden ser particularmente problemáticos en regiones áridas del suroeste de los Estados Unidos, en donde la calidad y cantidad del agua son temas polémicos. Cerca de 40,000 gansos Lesser snow (Chen caerulescens caerulescens) y gansos Ross (Chen rossii) invernan anualmente en el Refugio de vida silvestre Bosque del Apacbe, en Nuevo Mexico. Diariamente grandes cantidades de nutrientes son trasladadas de las granjas donde los gansos se alimentan a los humedales donde descansan. Mediante el uso de modelos de energía y balance de masas, estimaciones de la población, patrones de migración diaria y estacional y conductas alimenticias, estimamos la masa y proporción nitrógeno/fósforo de los nutrientes desgarrados por los gansos en los humedales del Bosque del Apacbe. Las tasas de descarga tuvieron picos al final de Noviembre de 1995 de >300 kg de nitrógeno y >30 kg de fósforo por día. Como la conducta alimenticia cambió a lo largo del invierno y las densidades de aves disminuyeron, las tasas de descarga cayeron. Nuestras estimaciones sugieren que en el invierno de 1995–1996 los nutrientes de origen avicola aportaron cerca del 40% del nitrógeno y 75% del fósforo que entró al humedal.

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mayormente utilizado por los gansos para descanso. Altas tasas de descarga por gansos son consecuencia de su conducta de descanso en colonias; >90% de los gansos descansó en solo 10% del área del humedal. Los efectos de descarga de nutrientes podrían ser reducidos incrementando las tasas de flujo o la dispersión de las aves en descanso. La pérdida de humedales naturales limita de cualquier manera las opciones para expandir el área de humedal disponible para las aves, además de que un incremento de las tasas de flujo puede ser difícil en esta árida región. Por lo tanto, el manejo de las aves y los nutrientes que mueven continuaría siendo un problema importante para los humedales en refugios de vida silvestre.

Introduction

The conservation and management of large waterfowl in North America have relied on the presence of wildlife refuges situated along major migratory routes. In western North America, Lesser Snow Goose (Chen caerulescens caerulescens) and Ross’s Geese (Chen rossii) migrate along the Pacific flyways from their arctic breeding grounds to winter in a series of managed wetlands in the southwestern United States and northern Mexico (U.S. Fish and Wildlife Subcommittee on White Geese 1992a, 1992b; Caithamer et al. 1995; Johnson 1996). Because of the loss of natural wetlands (Tiner 1984; Dahl 1990; Dahl & Johnson 1991) and increasing waterfowl populations (Boyd et al. 1982; Abraham et al. 1996; Ankney 1996), managed wetlands now sustain high densities of migratory waterfowl (Ankney 1996). The concentration of large numbers of birds into small managed wetlands is a major concern for refuge managers because it may promote the destruction of wetland vegetation (Lynch et al. 1947; Kerbes et al. 1990; Miller et al. 1996; Srivastava & Jeffries 1996); impose heavy losses on local agricultural crops (Hunt & Bell 1973; Bédard et al. 1986; Owen 1990; Van Eerden 1990); increase the risk of infectious disease outbreaks (Davis et al. 1971; Enright 1971; Wobeser 1981); and decrease water quality (Manny et al. 1994). Thus, evaluating the effects of high waterfowl densities on the wetland ecosystems that serve as over-wintering habitats is an important research focus for waterfowl conservation and wetland management.

The Bosque del Apache National Wildlife Refuge (NWR), situated in the middle Rio Grande Valley of New Mexico, provides wintering habitat for a number of the Ross’ and Lesser Snow Goose migrating along the Pacific flyways. This refuge now supports more birds than ever, including ducks, cranes, geese, shorebirds, and various raptors. During the winter, geese make daily feeding migrations that take them from roosting areas in managed wetlands to nearby agricultural fields in and around the refuge. These local migrations may be an important vector for the translocation of nutrients from terrestrial ecosystems (fields) to aquatic ecosystems (managed wetlands). The translocation and aggregation of nutrients by birds is important to a number of aquatic systems (Ganning & Wulff 1969; Bildstein et al. 1992; Manny et al. 1994; but see Bédard et al. 1980; Marion et al. 1994) and has been shown to affect nutrient cycling (Bazely & Jeffries 1989), primary production (Bosman et al. 1986), and intertidal community structure (Bosman & Hockey 1986; Wootten 1991). Little is known, however, about the role of nutrient translocation in wildlife refuges, where animals can reach high densities and where long-term conservation is paramount. Bosque del Apache NWR is also situated in a region where water is scarce, and the use of water by humans and wildlife is in potential conflict (Burton 1992). Thus, this refuge provides an example of the problems derived from the interaction of a limited water supply and high bird densities, and of how these problems may be exacerbated by the effects of nutrient loading by waterfowl.

Our objective was to estimate the nutrient inputs from geese into the wetlands of Bosque del Apache NWR. Using a combination of field observations and model simulations, we linked daily and seasonal migration patterns, population estimates, seasonal feeding behaviors, and mass and energy balance models to estimate daily and seasonal inputs of nitrogen (N) and phosphorus (P). These inputs were then compared with estimated N and P loads for the managed wetlands of Bosque del Apache. We also determined N:P ratios of inputs because water quality and water quality indicators (e.g., nitrogen-fixing cyanobacteria) are responsive to nutrient ratios (Smith 1983). Our results indicate that bird-borne nutrients are a considerable source of nutrients for the primary wetlands where geese roost.

Study Area

Bosque del Apache NWR is located in the southern portion of the middle Rio Grande Valley, about 156 km south of Albuquerque, New Mexico (33°48’ N, 106°53’ W; Fig. 1). The refuge currently has 24 wetland impoundments under moist soil management (Fredrickson & Taylor 1982), totaling about 494 ha along the west bank of the Rio Grande. Refuge wetlands are supplied with water through a complex system of canals and drains. Water is diverted into the refuge irrigation system at the refuge’s northern boundary from a combination of flows diverted directly off the Rio Grande, irrigation return
flows from agricultural fields, and ground water recharge accumulated in the Low Flow Diversion Canal. Unit 18d, the major roosting area for geese during the winter of 1995-1996, is a 50.2-ha wetland centrally located within the refuge (Fig. 1).

In addition to wetlands, the refuge administrators manage nearly 500 ha of agricultural fields (Fig. 1) used to grow corn and alfalfa for wintering waterfowl. These fields produce over 850 metric tons of corn and 460 metric tons of alfalfa per year as forage primarily for geese and Sandhill Cranes (Grus canadensis). Geese and cranes feed on loose fallen corn grains or pick corn grains from intact husks. Corn is actively managed to provide food for cranes and to discourage use by geese so that flocks will disperse northward to state refuges in the middle Rio Grande Valley. Initially, standing corn stalks are "bumped" (knocked down at about 0.75 m off the ground) to allow feeding by cranes. Bumped corn discourages feeding by geese because they are unable to see predators over the corn stalks. Then corn stalks are "mowed" (cut down at the base) to allow multi-species feeding. Corn is usually bumped in November or early December and then mowed in late December or early January.

### Methods

#### Population Trends, Local Migration Patterns, and Feeding Time

We used weekly ground counts to estimate goose and crane populations on Bosque del Apache NWR and throughout the middle Rio Grande Valley. During the 1995-1996 winter season, geese used upper valley state refuges, Bosque del Apache NWR, and the fields of two dairy farms in the upper valley exclusively. Cranes primarily used the same areas as geese but also used some private lands that were not surveyed. Surveys were begun at Bosque del Apache NWR by 1000 hours. We conducted the survey route northward from the refuge by car to known use areas and were generally finished by 1600 hours after covering 160 km. We estimated flock size using units of 50 or 100 individuals. Counts were tallied by survey area and then summed to provide population estimates for the entire wintering population of the middle Rio Grande Valley. Lesser Snow and Ross' Geese were not differentiated in counts, but Lesser Snow Geese were predominant in the population.

In 1995-1996 we used focal flock techniques (Davis et al. 1989) to determine the pattern of local migrations and the time spent feeding. Each week a focal flock that represented a large number of geese was followed from dawn to dusk. Each half hour we noted the location of the flock (agricultural fields or wetlands) and their behavior (feeding or loafing).

#### Nutrient Loading Model

We estimated N and P loading with a nutrient loading model that linked avian bioenergetics to seasonal feeding behaviors, daily and seasonal migration patterns, and refuge goose population estimates. Similar approaches have been used for estimating nutrient translocation by aquatic invertebrates and fishes (Kitchell et al. 1979; Kraft 1992; Schindler et al. 1993; Schindler & Eby 1997), burrowing organisms (Kitchell et al. 1979), and other bird populations (Bildstein et al. 1992). The bioenergetics model created a dynamic link between ambient temperatures and goose excretion rates and allowed us to estimate seasonal and historical changes in nutrient loading. We examined goose populations because they represent more than half of the total bird biomass wintering at the refuge, because their foraging behaviors are well-documented, and because other birds either do not leave the wetlands in daily feeding migrations (e.g., ducks) or may migrate to distant sites for extended periods (e.g., cranes).

Daily energy requirements for geese were estimated from the avian bioenergetics model of Kendeigh et al. (1977). The model incorporated the energetic costs of existence (basal) metabolism, routine metabolism of
free-living birds, and flight. The basic weight-dependent functions for existence metabolism (EM) were modified from Lasiewski and Dawson (1967). Existence metabolism was estimated as a function of bird mass and average daily temperature. At temperatures below 30°C, EM was estimated by linear interpolation from mass dependent functions estimated at 30°C and 0°C: at 30°C EM = 6.092 (mass^{0.628}), and at 0°C EM = 17.731 (mass^{0.532}), where mass is measured in grams and EM is in units of kilojoule per bird per day (Kendeigh et al. 1977). Free-living costs were estimated as a constant 7% of existence metabolism (Kendeigh et al. 1977), and flight costs were modeled as flight cost = 0.158 (mass^{0.47}) flight distance, where mass is measured in grams, flight distance in kilometers, and flight costs in kilojoule per bird per feeding trip (Kendeigh et al. 1977). Flight distance was estimated as the distance between unit 18d and the middle of the Bosque del Apache NWR agricultural areas (about 12 km round trip). The daily energy requirement (the sum of existence metabolism, free-living costs, and flight costs) was divided by the metabolizable energy coefficient (assimilation efficiencies) of food eaten (Table 1) to produce the total energy intake required to meet daily energy demands.

We assumed an average goose mass of 2630 g (average for Lesser Snow Geese; Dunning 1993) and that geese maintained a constant body mass through the winter (Ankney 1982). For the 2 weeks before spring migration we assumed a 5% premigration weight gain (0.35% per day; Ankney 1982). Geese were modeled as an equilibrium system in which the mass of food eaten equaled the mass excreted and respired (except during periods of weight gain). Mass of food eaten was calculated as the quotient of total energy consumed and the energy content of food eaten (Table 1). We assumed that premigration weight gain was primarily fat reserves and that geese did not store N and P. Consequently, we assumed geese were at equilibrium with respect to N and P.

Feeding behaviors of geese were estimated from weekly behavioral observations made throughout the middle Rio Grande Valley from early November to late February in 1988-1989. Our methods followed the flock-scan sampling techniques of Altman (1974) and Davis et al. (1989). Because geese often divided into many flocks using different habitats throughout the valley, scan samples were conducted in the habitat type where the majority of geese were present. When geese split into two nearly equal groups using different habitat types, we recorded geese behavior in both habitats. For modeling purposes we assumed that the wet mass of each diet item ingested was proportional to the time spent feeding on that diet item.

The mass of nutrients excreted was calculated from the total mass excreted and the N and P concentrations of food items ingested (Table 1). This represented the total amount of nutrients "passed through a goose," not the amount of nutrients loaded into refuge wetlands. The mass of nutrients loaded into wetlands was calculated as a function of total nutrients excreted, the gut clearance rate of each food type (Table 1), time spent feeding, and daily migration patterns of the geese. Nutrients derived from wetland plants (e.g., bulrush) were not included in our calculations of nutrient loading because they represented internal nutrient cycling. For consistency and clarity, we defined nutrients excreted as the total amount of nutrients excreted by geese and nutrients loaded as the subset of excreted nutrients that geese actually loaded into refuge wetlands.

The model was run at a daily time step. Individual excretion and loading rates (grams per bird per day) were multiplied by an estimate of refuge goose abundance. Goose numbers were estimated weekly, and daily abundance estimates were calculated by linear interpolation between weekly estimates.

### Table 1. Parameter estimates for corn, alfalfa, bulrush, and geese used in the nutrient loading model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen content (N)</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>14.4 µg N/g (wet mass) (^a)</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>8.3 µg N/g (wet mass) (^d)</td>
</tr>
<tr>
<td>Phosphorus content (P)</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>2.7 µg P/g (wet mass) (^a)</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>0.8 µg P/g (wet mass) (^d)</td>
</tr>
<tr>
<td>N:P ratio</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>5.3</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>10.4</td>
</tr>
<tr>
<td>Energy content</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>16.5 kJ/g (wet mass) (^a,b)</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>4.5 kJ/g (wet mass) (^a,b)</td>
</tr>
<tr>
<td>Bulrush</td>
<td>4.1 kJ/g (wet mass) (^a,b)</td>
</tr>
<tr>
<td>Goose</td>
<td>7.4 kJ/g (wet mass) (^c)</td>
</tr>
<tr>
<td>Digestion time</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>5%: 5.3 h (^b) 50%: 6.5 h (^b) 95%: 7.5 h (^b)</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>5%: 1.0 h (^b) 50%: 2.0 h (^b) 95%: 3.2 h (^b)</td>
</tr>
<tr>
<td>Metabolizable energy coefficient</td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>0.80 (^a,b)</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>0.34 (^b,f)</td>
</tr>
<tr>
<td>Bulrush</td>
<td>0.36 (^b)</td>
</tr>
</tbody>
</table>

\(^a\)Altman & Dittmer (1968). 
\(^b\)Karasov (1990). 
\(^c\)Cummins & Wuycheck (1971). 
\(^d\)Digestion time (or retention time) is the time in hours required for 5%, 50%, or 95% of a marked digestion item to be excreted. See Karasov (1990) for details. 
\(^e\)Estimated from 17 studies and seven nonpasserine bird species, including three spp. of geese, feeding on cultivated seeds, including corn (SD = 0.08).
\(^f\)Estimated from five studies and four nonpasserine bird species, including Snow Goose, feeding on alfalfa (SD = 0.03).
Daily meteorological data were collected from a meteorological station located at Bosque del Apache NWR and run by the Sevilleta Long Term Ecological Research site. The average of daily temperature readings (taken continuously over 24 hours) was used to estimate energetic requirements. The average daytime temperature (0800-1600 hours) and the average of maximum hourly wind speeds (taken hourly 0800-1600 hours) were used to predict local migration patterns. We used 0800-1600 hours because it represented the period in which geese were making foraging and flight decisions. We used the average of maximum hourly wind speeds because it was a better predictor of goose behavior than average wind speed.

Sensitivity Analysis

We conducted a sensitivity analysis of our nutrient loading model to test the influence of major assumptions and potential errors in forcing variables on annual loading. We systematically varied diet composition, population estimates, ambient temperature, free-living costs, flight distance, body mass, and local migration patterns. For body mass, free-living costs, flight distance, population estimates, and ambient temperature we varied each parameter or variable by ±10% for the entire winter season. For diet composition we varied the percentage of alfalfa in goose diets by ±10% on each day and the duration of time in fall that geese feed exclusively on alfalfa. For local migration patterns we varied the number of single-feeding-migration days by ±10%. All sensitivity simulations were run for the winter of 1994-1995, chosen because it had an average number of single-feeding-migration days (57).

Results

Population Trends and Local Migration Patterns

Geese arrive at Bosque del Apache NWR in late October and early November and depart by mid-March (Fig. 2). The number of geese at the refuge tends to decline in mid-winter as geese disperse to surrounding wildlife areas (Fig. 2). The magnitude and timing of the midwinter dispersal is, in part, a result of local crop management practices (Taylor & Kirby 1990). The number of geese wintering at the refuge increased from 1991-1992 to 1995-1996 (Fig. 2). In the winters of 1994-1995 and 1995-1996, Bosque del Apache NWR supported over 40,000 geese at peak densities.

Geese had two distinct, daily migration patterns. They made either one or two round trips per day to feed in agricultural fields. When making one feeding migration, geese flew to agricultural fields at dawn and remained there all day. They loafed on the fields during midday and returned to the wetlands at dusk. When making two feeding migrations, geese flew to the fields to feed in the morning and again just before dusk. During midday and at dusk geese returned to wetlands to loaf. These local migration patterns were similar to those observed for wintering Lesser Snow Geese (Davis et al. 1989) and Canada Geese (Branta canadensis; Raveling et al. 1972). During the day and at night, most geese loafed in one or a few of the managed wetlands. In the winter of 1995-1996, the vast majority of geese loafed in unit 18d during the day and at night.

The number of daily feeding bouts was related to environmental conditions. Average maximum daytime wind speeds (average of maximum hourly wind speed from 0800 to 1600 hours) and daytime temperatures were the best predictors of daily migration patterns (similar to Raveling et al. 1972). At high wind speeds, geese tended to make only a single feeding migration and therefore remained in the agricultural fields all day. Wind speeds at which geese switched from two feeding trips to one depended on temperature. At lower temperatures (<10°C), geese switched from two to one feeding trip at wind speeds 1.8 m/sec and higher (one trip median = 2.2, range 1.9-3.5 m/sec, n = 6; two trips median = 1.6, range 1.2-1.7 m/sec, n = 8), whereas at higher temperatures (>10°C) geese switched to one feeding trip at wind speeds of 2.4 m/sec and higher (one trip median = 3.1, range 2.5-4.1 m/sec, n = 5; two trips median = 1.7, range 1.2-2.2 m/sec, n = 4). When calculating nutrient loading rates, we used this relationship to determine which migration strategy geese were using.

Feeding Periods and Behavior

Regardless of daily migration pattern, geese fed twice per day, in the morning just after sunrise and in the after-
noon or evening just before sunset. The total amount of time spent feeding, however, varied with daily migration patterns. Geese spent more time feeding when making a single feeding migration (9.0 hours, \( n = 3 \), SD = 1) than when making two feeding migrations (6.0 hours, \( n = 11 \), SD = 1; one-way analysis of variance, \( df = 13 \), \( F = 22.7, p < 0.01 \)). Most of the difference in total time spent feeding resulted from longer periods of afternoon feeding when making a single feeding trip (4.0 hours, SD = 1.0) than when making two feeding trips (1.6 hours, SD = 0.5; \( F = 34.5, p < 0.01 \)). There was no significant difference in the amount of time spent feeding in the morning (5.0 hours, SD = 0, for one-feeding-trip days versus 4.4 hours, SD = 0.8, for two-feeding-trip days; \( F = 1.4, p = 0.25 \)). When calculating nutrient loading, we assumed that geese making a single feeding migration per day fed for 5 hours in the morning and 4 hours in the evening. Geese making two feeding trips per day fed for 4.5 hours in the morning and 1.5 hours in the evening. Although total daily food intake was determined by energetics (a function of temperature and body mass), the diet distribution of feeding—and therefore excretion—was derived from local migration patterns and time spent feeding. For example, when geese made two feeding trips, we assumed that 75% (4.5/6 hours) of the daily energy requirement was met by feeding in the morning and 25% (1.5/6 hours) was met by feeding in the evening. The timing of feeding was linked to calculations of gut passage time (Table 1) to provide estimates of where on the landscape, wetlands or fields, nutrients were excreted.

After arriving at Bosque del Apache NWR in the fall, geese spent the first 2 weeks feeding in wetlands on American three-square bulrush (Scirpus pungens; Fig. 3). As the bulrush was depleted, geese switched to alfalfa. After a few weeks the quality and quantity of alfalfa declined, and geese switched to a mixture of corn and alfalfa. During late December and early January, the coldest period of the year, the geese fed predominately on corn (Table 1). For modeling purposes we assumed that after week 6 (about mid-December) geese spent 59% of their time feeding on corn and 41% of their time feeding on alfalfa (the average for weeks 6 through 16).

### Table 2. Estimates of nitrogen and phosphorus excreted (passed through geese) and loaded (passed through geese and into a Bosque del Apache NWR wetland) for the winters of 1991–1992 to 1995–1996.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Nitrogen (kg/year)</th>
<th>Phosphorus (kg/year)</th>
<th>N:P ratio*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Excreted</td>
<td>Loaded</td>
<td>Excreted</td>
</tr>
<tr>
<td>1991–1992</td>
<td>11210</td>
<td>5540</td>
<td>1320</td>
</tr>
<tr>
<td>1992–1993</td>
<td>11880</td>
<td>6600</td>
<td>1370</td>
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<tr>
<td>1993–1994</td>
<td>12060</td>
<td>7200</td>
<td>1480</td>
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<tr>
<td>1994–1995</td>
<td>15920</td>
<td>7770</td>
<td>1760</td>
</tr>
<tr>
<td>1995–1996</td>
<td>15010</td>
<td>8780</td>
<td>1770</td>
</tr>
</tbody>
</table>

*N:P ratios (by mass) are given for guano excreted and loaded.
excreted in agricultural areas was derived from alfalfa because of its rapid gut passage rate.

A strong seasonal pattern existed in daily nutrient loading rates. Early in the season nutrient loading rates were very high, but they declined as goose densities decreased and as geese switched to a mixed diet of corn and alfalfa (Fig. 4). In 1995-1996 nutrient loading rates peaked in mid-November at 331.0 kg N/day and 31.8 kg P/day. The median loading rates for 1995-1996 were 38.6 kg N/day and 5.9 kg P/day.

The N:P ratio (by mass) of daily nutrient loading also changed seasonally. The N:P ratios declined from 10.4 in November and early December to around 6.5 for December through spring migration (Fig. 5). In February of 1995 we measured the N:P ratio of fresh goose guano at 6.8 (aggregate sample of more than 10 fresh, field-collected droppings from geese). The N:P ratios of nutrients loaded and nutrients excreted were the same in November and early December when geese fed exclusively on alfalfa, but later in the winter they diverged once geese switched to a mixed diet of corn and alfalfa. The cumulative annual N:P ratio of nutrients loaded was between 7.9 and 8.4, whereas the N:P ratio of nutrients excreted was between 8.5 and 9.0 (Table 2).

The ultimate distribution of loaded nutrients within the wetlands of Bosque del Apache NWR depended on the roosting habits of geese. In the winter of 1995-1996 a majority (>90%) of geese roosted on unit 18d. If all nutrients loaded were deposited in unit 18d (a 50.2-ha wetland), loading rates for 1995-1996 were 175 kg N/ha/year and 22 kg P/ha/year. In contrast, if geese were evenly distributed across refuge wetlands (approximately 500 ha of wetlands), loading rates would be only 18 kg N/ha/year and 2.2 kg P/ha/year.

Figure 4. Daily N and P loading rates by geese for the winters of 1991-1992 through 1995-1996. The months labeled on the x axis are October (O), December (D), February (F), and April (A).

Figure 5. Daily N:P ratio of nutrients excreted and loaded by geese in the winter of 1994-1995. The average annual N:P ratio of nutrients loaded is presented for comparison.

Sensitivity Analysis

Our nutrient loading model was relatively insensitive to our assumptions and forcing variables. Variation in population estimates had the greatest impact on nutrient loading estimates, with variation in nutrient loading equaling the 10% variation in goose numbers. For all other parameters, variation in nutrient loading was less than input variation. The N:P ratio of loaded nutrients was affected only by diet composition (+0.023% and −0.026%) and local migration patterns (±0.008%). In general, the most sensitive parameters were related to population estimates or behavioral patterns, all of which were measured directly.

Discussion

When aggregated in high densities, geese are capable of adversely affecting food availability and habitat quality (Lynch et al. 1947; Kerbes et al. 1990; Manny et al. 1994) and can have negative effects on co-occurring waterfowl. For example, high densities of giant nonmigrating Canada Geese have already been implicated in the decline of the Atlantic population of Canada Geese (Branta canadensis canadensis) and for poor gosling growth in the southern James Bay population of Canada Geese (B. c. interior; Ankney 1996). Furthermore, disease outbreaks, possibly resulting from high densities of geese and associated nutrient loading rates, would likely affect many waterfowl species (Davis et al. 1971; Bosque del Apache NWR, unpublished report). Rare and endangered populations, such as the Whooping Cranes (Grus americana) that winter at Bosque del Apache NWR (now fewer than 10 individuals), will be less able to withstand increased mortality.
Geese wintering at Bosque del Apache NWR redistribute large quantities of nutrients across the landscape. By feeding in numerous agricultural fields through the winter but roosting on a single wetland (unit 18d), geese aggregate nutrients from diffuse systems. The role of geese in the translocation and aggregation of nutrients is analogous to the role of bison (Day & Detling 1990), prairie dogs (Whicker & Detling 1988), and pocket gophers (Huntly & Inouye 1988) in grasslands, and the role of migratory and schooling fishes in marine (Meyer et al. 1983) and freshwater (Schindler et al. 1993) ecosystems.

The number of geese and their energetic demands, feeding behavior, and local migration patterns all influenced nutrient loading rates. Our model, however, was most sensitive to changes in population density. From year to year the number of geese wintering at Bosque del Apache drives the amount of nutrients loaded.

Geese feed primarily on corn and alfalfa. These food items differ considerably in terms of energy content, N:P ratio, and gut passage rates (Table 1). Consequently, feeding behaviors could have a large impact on both the amount and seasonal patterns of nutrient loading by geese. The metabolizable energy content (MEC multiplied by energy content) of corn is 8.6 times greater than that for alfalfa. To acquire the same amount of energy each day, a goose feeding on alfalfa must eat 8.6 times more alfalfa than corn, resulting in the excretion of 5.0 times more N and 2.6 times more P per day. Thus, changes in feeding behavior could have pronounced effects on the mass of nutrients loaded into the wetlands of Bosque del Apache NWR. Changes in local crop management that increase the proportion of alfalfa in geese diets—a reduction in local corn availability, for example—would increase the mass of N and P loaded. A diet of only alfalfa for the entire winter of 1995–1996 would have more than doubled N input (an additional 9700 kg of N) and would have increased P loading by over 60% (an additional 680 kg P).

Daily migration patterns can also affect nutrient loading rates. When making only one feeding migration, geese deposit most of the excreted nutrients on agricultural fields because they do not return to the wetlands at midday and because they spend more time feeding in the evening and therefore spend more time excreting in fields. Compared with geese making two feeding migrations per day, those making a single feeding migration load only 43% of the N and P when feeding on a mixture of corn and alfalfa and only 37% of the N and P when feeding exclusively on alfalfa. Loading rates are lower for geese feeding exclusively on alfalfa because of the shorter gut retention time of alfalfa. The cumulative effect of a large number of geese making only one feeding migration per day over many days is large. Had all the single-feeding-migration days been two-feeding-migration days, nutrient loading would have increased by nearly 2000 kg N (35%) and 250 kg P (36%).

The strong seasonal trend in daily N:P ratios was driven by shifts in diet composition. Alfalfa has a higher N:P ratio than corn (Table 1). The high N:P ratio of nutrients loaded occurred while geese were feeding exclusively on alfalfa. During this period, the N:P ratio of nutrients loaded into the wetlands and the N:P ratio of nutrients excreted were the same (Fig. 5). Daily N:P ratio then declined as geese switched to a mixed diet of alfalfa and corn. When geese fed on corn and alfalfa, the daily N:P ratio of nutrients loaded diverged from the N:P ratio of excreted nutrients (Fig. 5) because of the different retention times for corn and alfalfa. Because corn has a longer retention time, proportionally more corn was loaded per day than alfalfa and, therefore, N:P ratios of loaded nutrients were lower than those for excreted nutrients. Short-term (daily) fluctuations in the N:P ratios of nutrients loaded resulted from changes in daily migration patterns. The N:P ratios of loaded nutrients were lower on days that geese made a single trip to fields than on days when geese made two trips. The N:P ratios were decreased because more corn than alfalfa was loaded into the wetlands on single-feeding-migration days, again because of the longer retention time of corn.

The importance of geese as a nutrient vector can be judged only in the context of other major sources of nutrient input. Other potential inputs are surface- and groundwater flow, N fixation, and the wet and dry fall of nutrients. Calculations based on flow estimates and measured nutrient concentrations of inflow water (measured weekly in 1995–1996 from November to mid-March) indicate that surface water flow contributed around 13,000 kg N and 350 kg P to unit 18d from mid-November to mid-March. Estimates of wet fall for the Rio Grande region (National Atmospheric Deposition Program 1997, unpublished data) suggest loading rates of 2.9 kg/ha/year N or about 35 kg N total loaded to unit 18d from November to March. Dry fall probably adds another 50 kg N. For the same period, geese loaded 8780 kg N and 1090 kg P (Table 2), or around 40% of the N and 75% of the P input to unit 18d during the winter of 1995–1996. These estimates are probably high because N fixation and groundwater flow contribute an unknown amount of nutrients to unit 18d. Regardless, nutrients contributed by geese were roughly equivalent to surface water flow, the largest single input source for most wetlands (Kadlec 1979).

Bosque del Apache NWR is also the overwintering home for around 15,000 Sandhill Cranes. Like Snow and Ross’ Geese, Sandhill Cranes make daily feeding migrations between aquatic roosting sites and farm fields. Although we know much less about the migration and feeding behaviors of these cranes, our observations suggest that most overwintering cranes roost in cottonwood stands along the Rio Grande. Some cranes, how-
ever, roost in the managed wetlands of the refuge. In 1995–1996 we observed a few thousand cranes roosting with geese in unit 18d. Although the number of cranes is not high, because of their greater body mass (3.2 kg for Lesser Sandhill Cranes and 5.6 kg for Greater Sandhill Cranes; Dunning 1993), Sandhill Cranes excrete between 120% and 150% more nutrients per day than geese. This suggests that even a few thousand Sandhill Cranes may be contributing large amounts of nutrients to unit 18d and that we probably underestimate actual bird-borne nutrient loading rates.

Bird-borne nutrients should be biologically important to wetlands. Wetlands are generally considered N-limited or N- and P-collimited (Kadlec 1979), and birds contribute highly soluble forms of N and P (Bédard et al. 1980; Bosman & Hock 1986) that are readily absorbed by algae, bacteria, and aquatic macrophytes. Furthermore, N:P ratios below 29:1 by mass are known to promote the dominance of nitrogen-fixing cyanobacteria (Tilman et al. 1982; Smith 1983), which often indicates poor water quality (Lathrop & Carpenter 1992). Annual and daily N:P ratios of nutrients loaded were always below the 29:1 threshold. From November to February of 1995–1996, the N:P ratio in unit 18d averaged 20:1 (measured in outflow water), intermediate between that for inflow water (37:1) and estimates for bird-borne nutrients (8:1). This is additional evidence for the influence of bird-borne nutrients on the nutrient budget of this managed wetland. An ongoing study will further explore the effects of goose-contributed nutrients on the water quality and productivity of unit 18d and the wetland system of Bosque del Apache NWR as a whole (Kitchell et al. 1998).

**Implications for Conservation and Management**

The number of geese and Sandhill Cranes over wintering in the middle Rio Grande Valley has increased dramatically since the late 1960s (Fig. 6), paralleling trends observed across North America (Abraham et al. 1996; Ankney 1996) and Europe (Warren & Sutherland 1992). Over 45,000 geese and 20,000 Sandhill Cranes now overwinter in the middle Rio Grande Valley. Most of these birds feed and roost in and around Bosque del Apache NWR (Taylor & Kirby 1990). Although the rate of increase in goose and crane populations wintering in this region has slowed, populations are still increasing. Because nutrient loading rates are sensitive to waterfowl density, upward trends in goose and crane densities are conspicuous, if not of concern to managers (Ankney 1996).

The substantial nutrient loads derive from the strong colonial roosting behavior of geese. In this case over 90% of the goose roost on 10% of the available wetlands. If geese were spread across the wetland network, rather than concentrated in unit 18d, nutrient loading rates would be substantially reduced. This is important because, as goose populations continue to increase, nutrient loading rates may exacerbate water quality problems. Water-quality problems may, in turn, produce conditions suitable for outbreaks of avian cholera and type C botulism (Bell et al. 1955; Davis et al. 1971; Enright 1971; Wobeser 1981). Likewise, the occurrence of nitrogen-fixing cyanobacteria can cause direct toxicity, increase bird stress, and increase the likelihood of disease outbreaks (Codd 1995; Pizzolon 1996). Although unit 18d does not suffer from poor water quality under present flushing and loading rates, higher goose densities may demand additional management actions (Taylor & Kirby 1990). Re-distribution of geese across multiple wetlands or increased wetland flushing rates could reduce the localized effects of nutrient loading. The former requires actions that discourage communal roosting behaviors; the latter requires a sustained water supply and aggressive management of water distribution.

Waterfowl management has historically relied on wildlife refuges to support migratory birds at critical sites along major migration routes. In the southwest, in particular, managed wetlands are of critical importance to many species of waterfowl. The recent increase in goose numbers (Ankney 1996) and declining area of natural wetlands (Tiner 1984; Dahl 1990; Dahl & Johnson 1991) suggests that the importance of bird-borne nutrients will continue to increase in managed wetlands across North America. The specific effect of these nutrients will depend on a number of factors, but wetland area and hydrologic flushing rates will be particularly important. Because Bosque del Apache NWR is located in an arid region with expanding urban areas and water demand, water quality and quantity are contentious issues that may ultimately limit the flexibility of management options. Although water management efficiency at the ref-
uge has vastly improved, water shortages remain a constant concern in dry years. Furthermore, because of the loss of native wetland habitat to agriculture and urban expansion, the conservation of wintering waterfowl in the middle Rio Grande Valley relies almost exclusively on state and federal wildlife refuges (Taylor & Kirby 1990). Intensive management actions, including food and water management, hunting, and bird harassment, have been used to disperse birds throughout the middle Rio Grande Valley to more fully utilize the collective resources in state and federal refuges (Taylor 1992). Despite these actions, migratory birds still concentrate at various locations within this wintering area. Fewer options now exist for expanding the area of wetlands available to waterfowl in this region. Thus, management of geese and the nutrients they translocate will continue to be an important issue for the managed wetlands of waterfowl refuges.

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Literature Cited


